

Research review

An allometry perspective on crops

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Summary

Understanding trait–trait coordination is essential for successful plant breeding and crop modeling. Notably, plant size drives variation in morphological, physiological, and performance-related traits, as described by allometric laws in ecology. Yet, as allometric relationships have been limitedly studied in crops, how they influence and possibly limit crop performance remains unknown. Here, we review how an allometry perspective on crops gains insights into the phenotypic evolution during crop domestication, the breeding of varieties adapted to novel conditions, and the prediction of crop yields. As allometry is an active field of research, modeling and manipulating crop allometric relationships can help to develop more resilient and productive agricultural systems to face future challenges.

Introduction

For wild and cultivated species, body size is a key parameter of plant performance, fitness, and yield. Accordingly, plant size, expressed in terms of biomass, diameter or height, has considerably changed during evolution under cultivation (Fig. 1). On the one hand, early domestication and further diversification of landraces and varieties generally enlarged plants and their harvested parts, such as grains, fruits and leaves (Schwanitz, 1967; Evans, 1993; Meyer *et al.*, 2012; Milla & Matesanz, 2017; Gómez-Fernández & Milla, 2022). On the other hand, selection reduces plant height to facilitate fruit tree harvesting and avoids lodging in cereals (Hedden, 2003; Niklas & Marler, 2007). For instance, the introduction of dwarf genotypes in the 1960s by modern breeding enabled a massive increase in cereal yields under high-input agriculture, known as the Green Revolution (Donald, 1968; Khush, 1999; Hedden, 2003). Thus, selection for size has been essential in agriculture, with contrasting (but both successful) size-selection strategies in early and recent historical times.

Body size influences many aspects of organisms' physiology, morphology, and life history (Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1996). In plants, most phenotypic variance in adaptive traits is related to variability in whole-plant size (Díaz

et al., 2016). For instance, many traits related to biomass allocation, metabolic rates, and nutrient stoichiometry vary with global diversity in plant size (Niklas, 1994; Cornelissen, 1999; Aarssen & Jordan, 2001; Reich *et al.*, 2006; Díaz *et al.*, 2016). Moreover, genetic studies revealed that the genes controlling plant size jointly modulate many associated traits (so-called pleiotropic effects; see Guo *et al.*, 2010; Lim *et al.*, 2018). This suggests that trait–size relationships might reflect lines of least resistance along which genetic variation and selection primarily act. In crops, coordinated changes in plant size, morphology, and physiology are observed during the domestication of various species (Evans & Dunstone, 1970; Evans, 1993; Kluyver *et al.*, 2017; Milla & Matesanz, 2017). For example, plant size and harvested organ size tend to show parallel changes between ancestral and selected varieties in different types of crop species (Fig. 1). Consequently, as trait–size relationships have likely shaped current crop phenotypes, understanding them is crucial for predicting the impact of a change in one trait on the whole-plant phenotype during plant breeding. Furthermore, modeling of trait–size relationships in crop species allows us to understand to what extent human-assisted selection of specific crop features, such as high biomass allocation to reproduction, can manipulate trait–size relationships to improve crop performance.

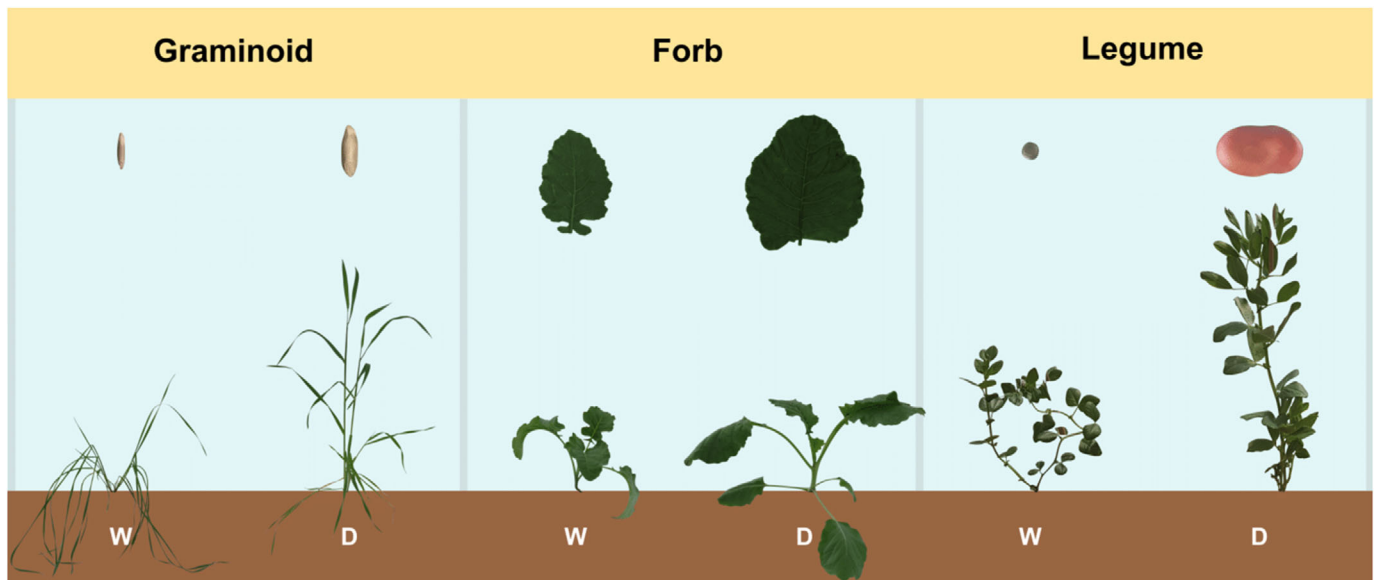


Fig. 1 Simultaneous changes in plant and organ size during crop domestication. Examples of size changes observed in a graminoid, a forb, and a legume crop type. From left to right: wild (W) and domesticated (D) wheat (*Triticum diccocooides* Schweinf., *Triticum durum* Desf.), cabbage (*Brassica oleracea* L.), and faba bean (*Vicia narbonensis* L. and *Vicia faba* L.). Whole-plant images are depicted at a consistent scale, harvestable organs are represented on scales specific to each crop. Further information on accession identities can be found in Gómez-Fernández *et al.* (2022).

In the past century, research into trait variation has revealed that traits often change disproportionately with increases in plant size (McMahon & Bonner, 1983; Schmidt-Nielsen, 1984; LaBarbera, 1989). This phenomenon is known as an allometric scaling relationship where the value of a given trait and size are functionally interconnected. Allometry refers to the proportional changes in the traits of an organism scales or changes in relation to plant size. Mathematically, this relationship between a given trait and size is often expressed as a power function (Huxley, 1924, 1932; Gould, 1966; Niklas, 1994; Calder, 1996) where:

$$Y = \alpha M^{\beta}$$

In this equation, Y is a plant trait that depends on the whole-plant mass M , α is a normalization constant that may vary between individuals or species, and β is the scaling exponent. The value of β is the slope of the relationship after log-linearization and indicates the nature of the trait change with respect to a change in plant mass. It describes whether traits change in direct proportion to body size (i.e. isometrically, $\beta = 1$) or allometrically (i.e. nonlinearly, $\beta \neq 1$) with plant mass. As discussed below, allometry is particularly valuable to crop breeders because it provides insights into how the selection of different traits can influence other traits and plant growth, which is crucial for optimizing crop yield, size, and resource allocation.

In the 1930s Kleiber (1932) observed that the metabolic rate of most animals scales to the $3/4$ of their mass (today known as the 'Kleiber's law'). More recently, a similar scaling relationship between size, growth, and metabolism, has been reported for plants (Enquist *et al.*, 1998, 2000; Niklas & Enquist, 2001). Remarkably, across diverse species and kingdoms, these scaling exponents exhibit a general consistency, often converging around approximate

quarter-power scaling exponents (e.g. $1/4$, $3/4$, $3/8$) (Kleiber, 1947; Banse, 1976; Niklas, 1994; Enquist *et al.*, 2000; Niklas & Enquist, 2001). This intriguing observation suggests that allometric relationships emerge from fundamental properties in the way organisms are built (Elgin, 2006; Sousa *et al.*, 2008; Glazier, 2014; Kempes *et al.*, 2019), which fostered the development of mechanistic theories to explain the seemingly apparent near-universality of many scaling relationships. For example, the surface area theory predicts a $2/3$ scaling exponent for how many traits and attributes, including metabolic rate and growth rate ($2/3$), population density ($-2/3$), and plant height ($2/3$), scale with changes in plant size, as a result of the disproportionate increase in volume with surface area (Rubner, 1883; White, 1981; Niklas, 1995; Dodds *et al.*, 2001). By contrast, the metabolic scaling theory (MST) predicts how numerous physiological and anatomical traits scale with allometric exponents that are multiples of a quarter (e.g. $-1/4$, $1/4$, $3/4$) based on the fractal organization of transport networks in multicellular organisms (Box 1). For instance, MST predicts a $3/4$ scaling exponent for the allometry of plant growth rate, which is consistent with observations across species and reflects that a plant 10 times larger is constrained to grow on average only 5.6 times faster, independently of the species and genotype. Extensions of MST also predict how the metabolic and growth exponent can vary due to differences in the scaling of the vascular network geometry and how this variation then influences the plethora of traits that covary with body size (Price *et al.*, 2007; Enquist & Bentley, 2012).

Statistical regularities in allometry suggest that biophysical laws strongly constrain trait–size relationships. Yet, as these relationships have not been extensively studied in crop species, whether crop traits scale with size as wild species remains unknown. Interestingly, there is a growing number of studies reporting scaling variability across and between species (White, 2010; Kozłowski

Box 1 Metabolic scaling theory

The metabolic scaling theory (MST) has been used to predict many trait–size relationships in plants (West *et al.*, 1997, 1999a,b; Enquist & Niklas, 2002; McCarthy & Enquist, 2007). The predictions of MST are based on the geometry of vascular branching transport systems that evolved in multicellular organisms to deliver nutrients to every metabolic-active cell (West *et al.*, 1997, 1999a). The theory posits that natural selection for energy-efficient nutrient delivery favored the evolution of space-filling, fractal-like transport structures in all multicellular organisms. The key predictions of MST are that, on average, plant growth rate scales isometrically to leaf biomass, ($\beta \approx 1$) and allometrically ($\beta \approx \frac{3}{4}$) with total biomass (Enquist *et al.*, 1998; West *et al.*, 1999b; Price *et al.*, 2007). Furthermore, numerous additional plant anatomical and physiological traits are predicted to covary with β such as plant respiration, photosynthesis, plant height, stem diameter, xylem conduit dimensions, biomass allocation, and plant density (West *et al.*, 1999b; Enquist & Niklas, 2002; Price *et al.*, 2007; Savage *et al.*, 2010; Enquist & Bentley, 2012; Deng *et al.*, 2012b). Many studies have tested MST predictions across plant species, and to a lesser extent, within plant species (Reich, 2001; Reich *et al.*, 2006; Duursma *et al.*, 2010; Vasseur *et al.*, 2012, 2018). These analyses allowed validating model predictions but also documented that some species and taxa deviate from the optimal $\frac{3}{4}$ scaling phenotype and that the scaling exponent for growth rate tends to change from isometric to allometric in small to large plants, across and within plant species (Enquist *et al.*, 2007; Mori *et al.*, 2010; Poorter *et al.*, 2015; Vasseur *et al.*, 2018). Relaxation of MST assumptions of space-filling or branching structure can begin to explain observed deviations from model predictions, suggesting that vascular network geometry can underlie scaling relationships (Enquist, 2002; Price *et al.*, 2007). Testing theoretical predictions with empirical data helps validate or invalidate theory assumptions, informing about the mechanisms shaping allometric relationships in plants.

et al., 2020; Glazier, 2022), and it is becoming increasingly clear that allometry is not only the result of biophysical constraints, but also the result of evolutionary processes such as natural selection (Enquist & Bentley, 2012; Vasseur *et al.*, 2018; Glazier, 2022; White *et al.*, 2022). Consequently, allometric relationships are also expected to respond to human-assisted selection, for instance to improve growth rate and seed yield by the selection of specific scaling parameters.

We advocate that allometric modeling might help understand how targeted outputs can – or cannot – be selected for in crop species. Such an approach has long been utilized in animals (Brody, 1964). Recent allometric studies in animal husbandry, including the domestication of chickens, pigs, and horses have been associated with changes in their scaling relationships (Evin *et al.*, 2015; Sánchez-Villagra *et al.*, 2017; Heck *et al.*, 2019; Núñez-León *et al.*, 2021). Moreover, chicken domestication was related to parallel changes between body, beak, and limb size, and modeling their allometry gave insights to enhance chicken breeds (Núñez-León *et al.*, 2021). In this article, we argue that developing a similar approach in crops can be powerful. First, we evidence that allometric relationships have shaped crop evolution during plant domestication. Then, we highlight to what extent modeling allometric relationships could give new opportunities for crop

improvement. Finally, we discuss how modeling crop allometries can help predict optimal crop performance in the field when grown in monoculture or under diversified conditions.

Evolution of plant allometry over the course of crop domestication

The domestication syndrome entails common phenotypic changes observed during the domestication of several species, such as enlarged harvestable organs, loss of natural seed dispersal, and decreased seed dormancy (Vavilov, 1951; Hammer, 1984; Evans, 1993; Fuller, 2012; Meyer *et al.*, 2012). The domestication syndrome also includes modifications in biomass allocation patterns with crops generally allocating a higher proportion of total biomass to the harvested part than their wild progenitors (i.e. crops have a higher harvest index, Evans, 1993; Hay, 1995; Berrocal-Ibarra *et al.*, 2002; González-Paleo & Ravetta, 2012; Royo *et al.*, 2021). However, as allometric relationships reflect (predictable) changes in biomass proportions with size (Coleman *et al.*, 1994; McCarthy & Enquist, 2007; Weiner *et al.*, 2009; Poorter & Sack, 2012), to what extent shifts in biomass allocation during domestication resulted solely from allometric changes remains an open question (see McCarthy & Enquist, 2007; e.g., the so-called ‘passive’ plasticity, Wang *et al.*, 2020). For instance, Qin *et al.* (2016) found a unique isometric relationship between root and shoot biomass across crop species, as predicted by MST theory (Enquist & Niklas, 2002), suggesting that root : shoot ratio evolved in crops following predictable allometric equations. However, other studies reported changes in plant allometry between wild progenitors and modern varieties in different crop species (Niklas & Marler, 2007; Milla *et al.*, 2014; Pedrosa *et al.*, 2018; Roucou *et al.*, 2018). For instance, significant differences in allometric coefficients of plant diameter-height and seed mass-fruit mass relationships were reported in papaya and Amazon tree grape (Pedrosa *et al.*, 2018), suggesting that domestication and selection altered crop allometries. Although a similar scaling exponent between crops and wild species was also found for the seed mass-seed coat allometry, the lower intercept across crops may have resulted from selection for decreased seed dormancy (Milla *et al.*, 2024).

The impact of domestication on plant growth rate has recently been carefully addressed (Simpson *et al.*, 2017; Gómez-Fernández *et al.*, 2022; Gómez-Fernández & Milla, 2022). These studies showed that the improvement of plant growth rate has not been homogeneous across species, as it depended on their domestication history. However, a re-analysis of published data from 19 crop species revealed that, on average, crop growth rate scales with an exponent indistinguishable from the predicted $\frac{3}{4}$ exponent (Fig. 2a,b), which would suggest similar constraints on the evolution of growth rate. At least, this indicates that crop species do not differ in their scaling from noncrop species and generally conform to the allometric relationship for growth rate predicted by MST. Moreover, wild ancestors, landraces, and elite lines shared a common growth rate-size relationship (Fig. 2b), which suggests that allometry has not been changed upon domestication. Despite a general adherence of crops to the MST prediction, our re-analysis also showed that the scaling exponent varied significantly between

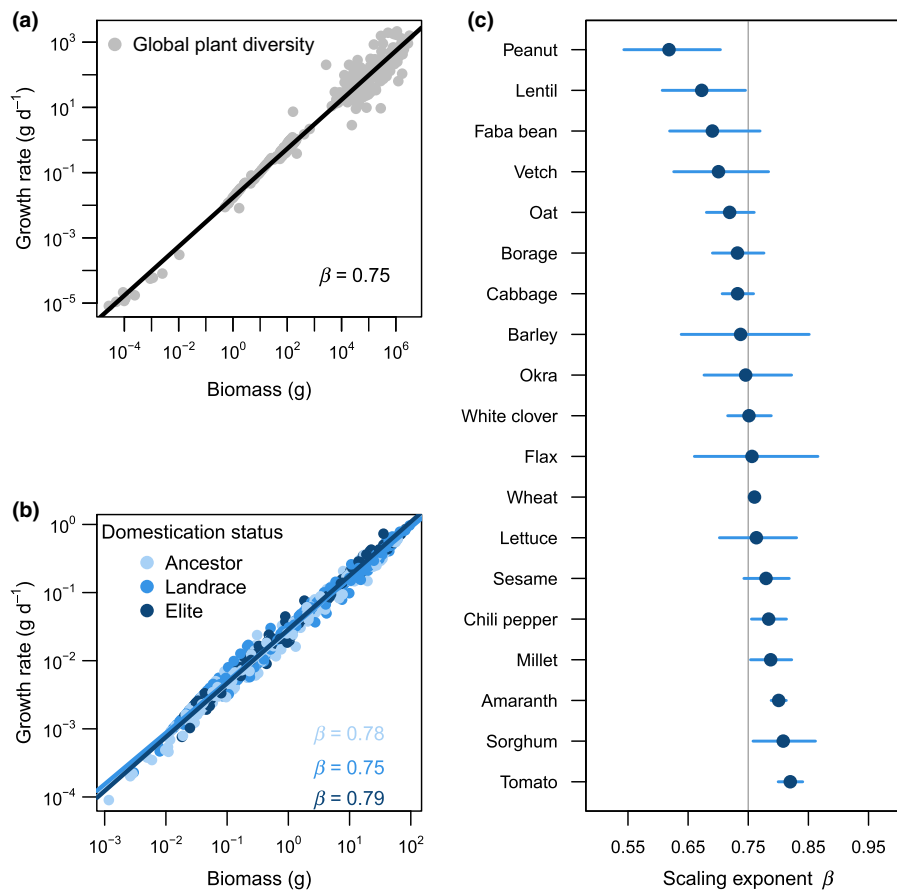


Fig. 2 Variation in crop growth rates explained by scaling relationships. (a) The previously reported scaling exponent (β) of $\frac{3}{4}$ for growth rate across a wide range of plant sizes found by Niklas & Enquist (2001). (b) Allometric re-analysis of the crop growth–plant size relationship at different stages of evolution under cultivation, using the data of 19 crop species from Gómez-Fernández *et al.* (2022). Three main domestication statuses can be distinguished (Abbo *et al.*, 2014; Gómez-Fernández *et al.*, 2022): ancestors, the closest wild relatives; landraces, domesticated genotypes that have not undergone intensive breeding in the last century; and elites, genotypes from more recent breeding programs (post-World War II). For each crop and domestication status, growth and size data were obtained from at least two different accessions representing crop diversity (for more information on accession identities, see Gómez-Fernández *et al.*, 2022). Differences in scaling parameters between wild progenitors, landraces, and elites were not statistically significant. (c) Variation in scaling exponents for the plant size–growth rate relationship between crop species. Crop species were ordered by increasing mean scaling exponent from top to bottom. Crop-specific scaling exponents ($\pm 95\%$ confidence intervals) were calculated by reanalyzing landrace and elite data for each species from Gómez-Fernández *et al.* (2022). The vertical line represents the $\frac{3}{4}$ scaling exponent predicted by the metabolic scaling theory (MST). Allometric analysis was performed with standard major axis tests using the *SMATR* R package (Warton *et al.*, 2012).

crop species around the predicted $\frac{3}{4}$ exponent (from $\frac{2}{3}$ to $\frac{4}{5}$; Fig. 2c). As such, more experimental studies are needed to unveil how crop-specific variations in the scaling exponent relates to crop type and domestication history. Nonetheless, these results indicate that domestication has been strongly constrained by allometry. Together, these findings illustrate that domestication has modified specific allometric relationships, and not all. Whether modern selection can still operate on plant allometries, on which relationships and to what extent, is a critical question for future crop improvement.

Plant allometry: constraint or promise for plant breeding?

Relatively conserved allometric relationships among crop and wild species (as in Fig. 2b) may indicate that trait–size

relationships represent an optimum in the fitness landscape, constraining the evolution of new phenotypes along the allometric line (Olson, 2012). Interestingly, beyond growth rate, allometric theories also make predictions about how traits such as biomass allocation change with plant size. For instance, MST predicts that leaf mass, stem diameter, and root mass scale with whole-plant mass as the $\frac{3}{4}$, $\frac{3}{8}$, and 1, respectively (Enquist *et al.*, 1998, 1999; Enquist & Niklas, 2002). Moreover, power law equations also generally describe allocation to and in reproductive tissues such as seed or fruit weight and their quality in terms of protein, sugar, or nitrogen content (Samson & Werk, 1986; Martre *et al.*, 2003; Niklas & Enquist, 2003; Niklas, 2006; Rotundo *et al.*, 2009; Weiner *et al.*, 2009; Plessis *et al.*, 2013). Often there is no clear prediction for scaling exponents related to reproductive traits, presumably because the associated relationships are more variable and taxon-specific. This questions to what extent biomass

allocation in crops, notably the biomass allocated to the harvested part, can be predicted by allometric theory. The few studies investigating allometric relationships for biomass allocation in crop species found MST-predicted scaling exponents for root–shoot allocation or stem–leaf mass allocation, as observed in wild species (Qin *et al.*, 2016; Milla & Matesanz, 2017). These promising findings open new avenues for predicting optimal crop performance with allometric models. Simple allometric equations could offer a valuable alternative, or complement, to complex crop models requiring many parameters. However, further analyses and experiments are needed to test this approach. One main limitation is that measuring traits related to plant allometry (i.e. size, biomass allocation, and physiological rates at the *individual* level) is experimentally laborious, which prevents comparative studies across a large range of varieties. However, the growing capacities of high-throughput phenotyping facilities combined with technological development (Granier *et al.*, 2006; Flood *et al.*, 2016; Tardieu *et al.*, 2017; Reynolds *et al.*, 2019; Volpato *et al.*, 2021), now leverage our ability to analyze multiple crop species and varieties, which opens the door to the use of allometric models for crop performance prediction. For instance, allometry was recently used to predict fruit development from ovule protein concentration in eight crop species (Colombié *et al.*, 2023).

If allometric relationships are strongly constrained and poorly variable, the range of trait combinations that plant breeders can create and use for varietal improvement might be limited. However, genetic variation at the intraspecific level for scaling parameters has now been strongly documented (Glazier, 2005; Chmura *et al.*, 2017; Careau & Glazier, 2022), which can provide new opportunities for plant breeding. For example, high heritability (broad-sense $H^2 = 0.95$) for variation in the growth rate–size scaling exponent was found in the plant *Arabidopsis thaliana* (Vasseur *et al.*, 2018). In addition, recent works suggest that variation in the scaling exponent is associated with variation in plant performance and stress resistance (Muir & Thomas-Huebner, 2015; Vasseur *et al.*, 2018). In *A. thaliana*, deviations from $\frac{3}{4}$ scaling decreased seed production and increased stress resistance (Vasseur *et al.*, 2018). Is variation in scaling exponents among crop varieties similarly associated with the optimization of different components of performance? Answering this question might become critical to adapt crop varieties to future climate. Allometric engineering, that is experimentally changing scaling parameters, has been proposed to test the impact of allometric deviation on performance (Sinervo & Huey, 1990; Olson, 2012). In addition, artificial selection experiments on allometric parameters are expected to be a powerful approach to test the links between scaling variation and fitness traits, its genetic architecture, and its response to selection (Conner, 2003; Frankino *et al.*, 2005; Egset *et al.*, 2012; Pélabon *et al.*, 2014; Voje *et al.*, 2014; Bolstad *et al.*, 2015; Houle *et al.*, 2019). For instance, increased yields during recent plant breeding have been accompanied by a modulation of allometric relationships for biomass allocation in soybean (Tamagno *et al.*, 2020), oats (Semchenko & Zobel, 2005), and wheat (Qin *et al.*, 2013). We firmly believe that investigating the links between allometric variation and yield has a great power

for crop improvement and crop modeling. We highlight below possible avenues in that direction.

First, we need to screen for genetic variation in allometric parameters by analyzing trait–size variation at a particular phenological stage, during ontogeny or in response to environmental gradients (Fig. 3). For instance, by examining the residuals of the relationships, we can analyze allometric variation as the departure of peculiar genotypes from the global allometric relationship (Fig. 3, middle panel). Moreover, if the allometric relationship exhibits nonlinearity after log-linearization, which has been frequently reported across and within species (Enquist *et al.*, 2007; Kolokotronis *et al.*, 2010; Mori *et al.*, 2010; Vasseur *et al.*, 2012, 2018; Poorter *et al.*, 2015; Zhou *et al.*, 2021), this indicates variation in slopes (i.e. in allometric exponents) between genotypes (Fig. 3, middle panel). Quadratic models better fit nonlinear allometric relationships, and the derivative of the model measures the variation of allometric exponent between genotypes (Kolokotronis *et al.*, 2010; Vasseur *et al.*, 2018). As higher scaling exponents reflect a more-efficient trait increase per unit biomass, investigating such intraspecific variation may be critical to improve future crop varieties. As many traits vary dynamically with size during development (such as biomass allocation see McConaughay & Coleman, 1999; Poorter & Sack, 2012), allometric models can be used to detect genetic variation for trait trajectories during ontogeny or in response to the environment (Ma *et al.*, 2002; Long *et al.*, 2006). The use of allometric models allowed to identify many quantitative trait loci (QTL) regulating biomass allocation patterns during ontogeny, including stem and seed mass (Li *et al.*, 2007; Huang *et al.*, 2014; Jiang *et al.*, 2016). As such, breeders can select for genotypes having more or less ‘stable’ trajectories during the season (Fig. 3, right panel), which may be interesting to govern yield stability. In addition, genotypic responses to an environmental gradient can be analyzed from an allometric perspective. For instance, when different genotypes are grown in contrasting levels of resource availability, this will impact their size and traits following scaling equations (Fig. 3, right panel). Indeed, it is known that allometric parameters may change between different environments, such as with water (Eziz *et al.*, 2017) or nutrient availability (Semchenko & Zobel, 2005; Li *et al.*, 2017). The parameters of these equations determine allometric reaction norms, which inform about the sensibility of a genotype to a particular environmental stress. For instance, changes in plant density revealed genotype-specific allometries for reproductive allocation in wheat, maize, soybean, and sunflower, informing how the harvest index changes with plant density (Vega *et al.*, 2000; Weiner *et al.*, 2009; Qin *et al.*, 2013; Du *et al.*, 2020). Therefore, allometric models have the power to jointly compare the traits of genotypes in optimum conditions and in response to stress. As a proof of concept, recent studies characterized genetic variation for shade-avoidance responses in wheat by studying allometric slopes (Zhang *et al.*, 2023; Golan *et al.*, 2024). Altogether, different methods can be used to screen for genetic variation in scaling parameters affecting different components of crop yield.

Second, we need to resolve the genetic determinants of trait–size relationships and allometric coefficients. The genetic determinism of allometric relationships recently started to be elucidated, but the

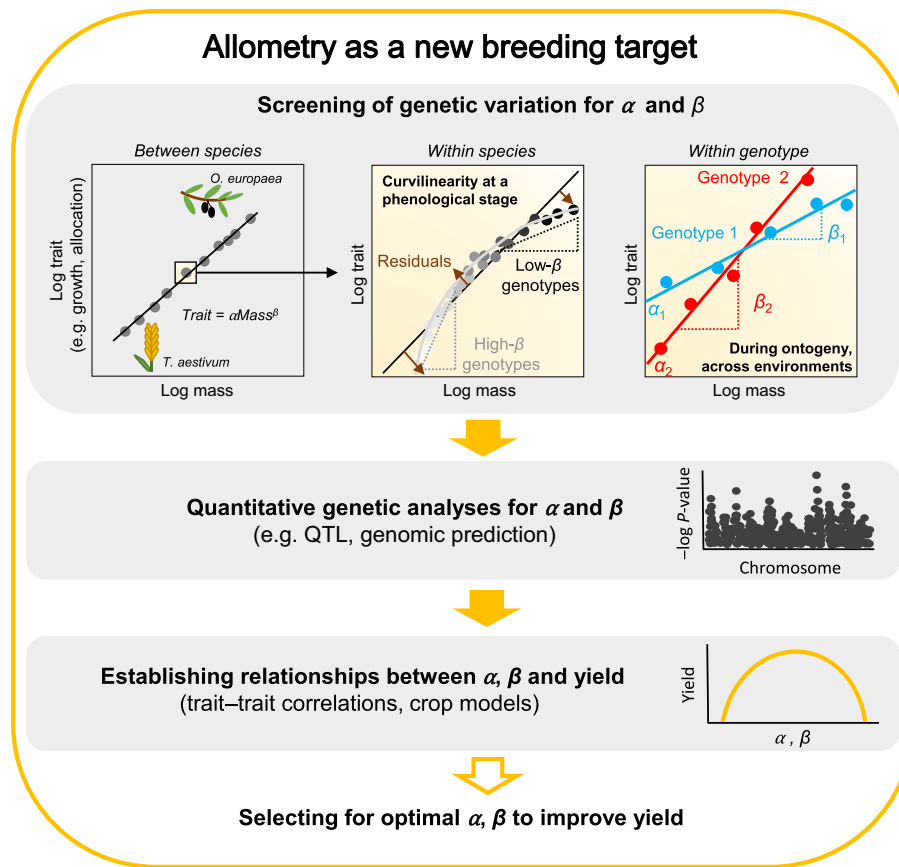


Fig. 3 Allometry as a new breeding target. Three-step framework outlining how to use intraspecific allometric variation as a breeding target. First, trait–size variation is screened across and within species. Across species (left panel), allometric relationships are continuously tested with trait–size data in wild and cultivated species to analyze the adherence of species to global patterns in trait–size variation. Within species (middle panel), a population of genotypes is screened for variation in scaling parameters – normalization constant (α) and scaling exponent (β) – of a given trait. For example, trait–size variation within a species often shows nonlinearity at a particular phenological stage (also called static allometry by Cheverud, 1982; see Vasseur *et al.*, 2012, 2018). Next to scaling parameters, the residuals of the relationships can be analyzed as the departure of genotypes from the global allometric relationship (middle panel, see Wuest *et al.*, 2022). Within genotypes (right panel), scaling relationships during growth (so-called ontogenetic allometry, Li *et al.*, 2007) or in response to environmental conditions (Qin *et al.*, 2013; Du *et al.*, 2020) may vary between genotypes. For example, impaired growth in sub-optimal conditions leads to reduced trait value, such as allocation to reproduction being less strongly in genotype 1 (blue line) than in genotype 2 (red line). After screening of allometric variation between genotypes, genetic association studies can be carried out in order to identify underlying genomic determinants, for example quantitative trait loci (QTL) or SNPs, and genetic architecture (Li *et al.*, 2007; Plessis *et al.*, 2013; Huang *et al.*, 2014; Vasseur *et al.*, 2018; Zhang *et al.*, 2020). Finally, the impact of scaling variation in α and β on performance (yield and its components) can be evaluated in the field (including effective field networks) or with allometry-enriched crop growth models (Messina *et al.*, 2011; Vasseur *et al.*, 2018). Together, genetic determinants of allometric parameters and their relationships with yield can be manipulated and/or used in gene-to-phenotype models during the breeding process that now explicitly incorporate allometry as a breeding target.

molecular mechanisms of coordinated changes in size and traits still need to be investigated (Vasseur *et al.*, 2022). Quantitative analysis of genetic variation in allometric coefficients offers a promising avenue to help breeders to identify genes that modulate yield, productivity, and competitiveness through allometric relationships. For instance, single-nucleotide polymorphisms (SNPs) have been identified explaining coordinated changes in plant and organ size (Guo *et al.*, 2010; Lim *et al.*, 2018; Vicente *et al.*, 2023), such as seed weight and plant height in barley (He *et al.*, 2023). It has been argued that scaling relationships at whole-plant level may be controlled by mechanisms operating at lower organizational levels, generating allometries from cell size to whole-plant size (Bennett, 1987; Gregory, 2002; Kozłowski *et al.*, 2003; Starostová

et al., 2009; John *et al.*, 2013; Mueller, 2015; Roddy *et al.*, 2020; Bestová *et al.*, 2021). Interestingly, genes controlling cell size, such as transcription factors (e.g. YABBY, MYB, and bHLH) influenced yield-related traits in crop species (Cong *et al.*, 2008; Wilkins *et al.*, 2009; Nicolas *et al.*, 2013; Lim *et al.*, 2018). Cell size was also related to enlarged organ size during domestication as a result of genome-doubling by polyploidization (Dunstone & Evans, 1974; Evans, 1993; Fang & Morrell, 2016; Salman-Minkov *et al.*, 2016). Indeed, positive scaling relationships between cell and genome size have been described across plant species (Mowforth & Grime, 1989; Kozłowski *et al.*, 2003; Knight & Beaulieu, 2008), but not yet at the intraspecific level. Interestingly, genome size variability was related to leaf traits in maize (Tenaillon *et al.*, 2011; Díez

et al., 2013), suggesting that scaling relationships at lower levels of organization influence trait variation at higher levels within species. Our growing understanding of the genetic determinism of allometric relationships paves the way for selection on scaling parameters as a way to manipulate the additive genetic values of growth rate, biomass allocation, and stress resistance. Moreover, allometric models can also be useful to improve the breeding of hybrids, which have long been key agronomical innovations in agronomy (Box 2).

Third, we need to evaluate the impact of scaling variation on crop performance in field conditions (Fig. 3). Increased scaling exponents for reproductive allocation in soybean varieties released between 1980 and 2013 (Tamagno *et al.*, 2020) suggest that scaling exponent variation may have been used by breeders to improve previous yields. Until now, how scaling parameter variation links to field performance is unknown. However, in cereals, genetic

variation in allometric coefficients has been related to yield stability across environments (Du *et al.*, 2020; Weiner *et al.*, 2021): A low scaling exponent (Fig. 3, blue line) may have greater yield stability compared with a high scaling exponent (Fig. 3, red line). In addition to correlation of scaling variation with performance, allometry-enriched crop growth models may be used to predict the impact of scaling variation on yield. After the evaluation of scaling variation on crop performance in the field, genomic prediction methods can be used to predict genotypic values for alpha and beta (Fig. 3) and assist in selecting those genotypes with the best set of scaling parameters for success in a given environment.

Scaling up to crop field performance

Allometric models have been developed to scale up from individual traits to population- and ecosystem-level features (Brown

Box 2 Prediction of hybrid vigor using allometry

Hybrids are expected to exhibit higher growth, disease resistance, and fertility than their parents (Crow, 1998). This phenomenon, called hybrid vigor or 'heterosis', is widely observed and agronomically exploited in plants and animals (Chen, 2010). Heterosis is quantified by the phenotypic deviation of a hybrid compared with the mean or best parental value, reflecting the nonadditive inheritance of the trait. However, the underlying mechanisms continue to puzzle biologists. As early as 1934, Wright proposed a model based on trait relationships to explain the metabolic deviation of hybrids at the cellular level. Wright's model was based on the relationship linking the concentration of enzymes to the metabolic flux that integrates their activity. Given that this relationship is nonlinear, the metabolic flux is expected to deviate ($Y_{Aa} > Y_{\text{mean}}$, Fig. 4) even if enzyme concentrations are additively inherited ($M_{Aa} = M_{\text{mean}}$). Recently, Fiévet *et al.* (2018) validated this approach by demonstrating that the enzyme–flux relationship can be modelled to predict hybrid variability for glycolysis in yeast. Interestingly, Wright tackled the problem of heterosis by exploring the geometry of trait relationships at different levels of phenotypic integration. Indeed, Wright's model suggests that hybrid deviation can be quantitatively explained by the curvature of trait relationships between two levels of phenotypic integration (also called Jensen's inequality). However, this approach has been completely ignored in studying complex trait inheritance in plants, such as those related to crop yield. This is mainly because, until recently, we lacked a mathematical framework to model complex trait variation and covariation. Yet, allometric models of trait relationships have considerable promise to scale up Wright's model of hybrid deviation to higher integration levels.

Due to the nonlinearity of allometric relationships (when traits are not log-transformed; solid black line, Fig. 4), the hybrid is expected to exhibit a higher Y value than predicted from a linear relationship (dashed black line), assuming additive inheritance for plant biomass. For instance, growth–size relationships were successfully used to predict the heterosis in *Arabidopsis thaliana* hybrids (Vasseur *et al.*, 2019). This case study in a model species suggests that testing the ability of allometric relationships to explain and predict hybrid vigor in crop plants represents a critical challenge to accelerate varietal improvement and optimize field performance in the near future.

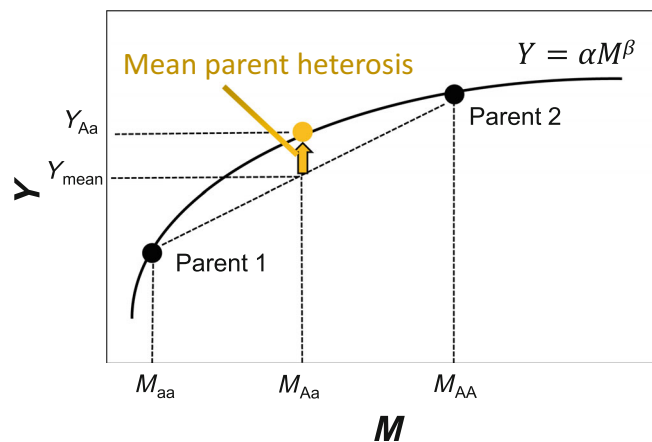


Fig. 4 Using nonlinearity of allometric relationships to predict mean parent heterosis. The nonlinear relationship between a trait (Y) and plant size (M) enables to predict mean parent heterosis in Y in the offspring (M_{Aa}) of a cross between two parents (M_{aa} , M_{AA}). The figure is based on the model presented in Vasseur *et al.* (2019).

Box 3 Allometry in crop models: current usage and future promises

Crop models are built to simulate plant growth, development, and yield under various field conditions (Monteith, 1977; Brisson *et al.*, 2003; Jones *et al.*, 2003; Keating *et al.*, 2003; Soltani *et al.*, 2013; Chenu *et al.*, 2017; Messina *et al.*, 2022). Mechanistic crop models typically use climatic variables to simulate plant processes such as temperature to simulate leaf area development that, in turn, determines how much light is transformed into biomass. Then, the developmental stage or a trait–size relationship determines how biomass is distributed to roots, leaves, stems, or grains (Marcelis *et al.*, 1998). For instance, trait–size relationships are used by the SSM-iCrop model to predict biomass allocation to leaves (Soltani *et al.*, 2013) and by the APSIM model to predict the number of grains (Zheng *et al.*, 2014). However, these trait–size relationships have until now not been linked to the field of plant allometry and mechanistic theory such as for biomass allocation by the metabolic scaling theory (MST, Niklas & Enquist, 2002; Enquist & Bentley, 2012). In addition, emergent trait–size properties from existing crop growth models could be compared with theoretical expectations of MST to test their consistency (Peaucelle *et al.*, 2019). For example, modeling how different plant sizes or densities impact biomass yield could be compared with their MST predictions. Next, allometric relationships may simplify current crop models due to their low parameter number, responding to the demand for parsimonious models to facilitate high-speed simulations (Hammer *et al.*, 2019). As such, allometric relationships for traits such as phenology (Marba *et al.*, 2007; Fournier *et al.*, 2020) and plant density (Deng *et al.*, 2012b) could be integrated to create allometry-enriched crop growth models. Subsequently, genetic variation in scaling parameters can be used to parametrize these allometry-enriched crop models to predict genotypic performance (see Fig. 3). For example, cultivar-specific allometric models between leaf, stem mass, and branch cross-sectional area are used to predict growth and reproduction in mango (Normand & Lauri, 2012). The coupling of genetic analysis (e.g. genomic prediction) with allometry-enriched crop models creates integrative gene-to-phenotype models that can efficiently predict crop performance in multiple environments (Hammer *et al.*, 2006, 2010; Messina *et al.*, 2009, 2022; Technow *et al.*, 2015; Diepenbrock *et al.*, 2022; Onogi, 2022). As variation in a single scaling parameter can drastically impact plant performance, they represent an effective and parsimonious set of parameters to predict the performance of thousands of genotypes across many years and locations within a short time span. Together, we anticipate that an allometry perspective can complement mechanistic crop models to foster the development of high-speed crop models directing crop management and breeding efforts.

et al., 2004; Price *et al.*, 2010). Even if the mechanistic bases are still unclear, the scaling up from individual to ecosystem also displays statistical regularities, which offers testable predictions regarding resource allocation and yield optimization in different management scenarios. For example, the density of organisms per unit area scales with organism body mass (M) following a power law equation with a scaling exponent that is either $c. -2/3$, based on the surface area theory, or $-3/4$, based on MST (White, 1981; Deng *et al.*, 2008). This size dependency of plant density is known as the self-thinning rule (White, 1981). Furthermore, MST predicts that standing biomass per unit land area increases as $M^{1/4}$ and canopy growth as M^0 (Enquist *et al.*, 1998; Brown *et al.*, 2004). These

equations are used to predict features of ecosystems that were previously inaccessible such as how forests influence global carbon and water cycles (West *et al.*, 2009; Coomes *et al.*, 2012). Recently, MST predictions for density and biomass production were empirically confirmed across a range of crop species and allowed to determine the optimal density to maximize biomass yield (Deng *et al.*, 2012a,b). Allometric relationships were also used to determine nitrogen fertilization rate in crops (Sadras & Lemaire, 2014; Lemaire *et al.*, 2019) or to quantify plants' stress levels (Anfodillo *et al.*, 2016). This suggests that allometric models can be used at farm level to aid in decision-making. However, although existing crop growth models already use allometric relationships, allometry remains limited to crop models until now (Box 3). We propose to extend the framework of Deng *et al.* (2012a) with allometric relationships for biomass allocation to predict grain yield. In Box 3, we review how crop models currently use plant size relationships and describe how allometric theory and scaling parameter variation can facilitate the modeling of crop performance in the field.

Adaptive variations that optimize yield at the field level can be associated with different size-selection strategies. In most species, higher plant size is expected to be associated with higher reproductive output. Accordingly, larger and more competitive plants have been selected during domestication and early evolution under cultivation (Milla *et al.*, 2014; Montazeaud *et al.*, 2020). However, as bigger plants compete more with each other (Violle *et al.*, 2009), smaller and less competitive plants can also improve the group's performance (Donald, 1968; Jennings & de Jesus, 1968; Weiner *et al.*, 2010). For instance, selection for communal traits such as shortened stems contributed to yield increases during the Green Revolution and recent varietal improvement (Anten & Vermeulen, 2016; Perez *et al.*, 2019; Weiner, 2019). Furthermore, more vertically oriented leaves reduce the individual plants' competitive ability but avoid light saturation and enable higher photosynthesis in the plant's lower leaves, thereby improving light-use efficiency at the canopy level (Zhu *et al.*, 2010; Perez *et al.*, 2019; Messina *et al.*, 2023). Accordingly, recent plant breeding efforts aim to breed against natural selection for competitive genotypes to increase yield at the population level (Weiner, 2019; Montazeaud *et al.*, 2020). In Box 4, we propose an MST-inspired framework to evaluate how plant breeding for communal traits may have impacted the allometry between size and plant density to increase yield during the Green Revolution. Using such a framework might help understanding which traits facilitated previous yield increases, as well as which factors impacting the size–density relationship allows maximizing crop yield in different species.

Allometry perspective for crop diversification: genotype combination, intercropping, and crop mixtures

Cooperating phenotypes are expected to be particularly efficient under high-density monoculture systems, but less under more diversified conditions. This is because cooperating plants, such as communal plant types that increase light-use efficiency, allowing

Box 4 The Green Revolution through the lens of allometry theory

During the Green Revolution, agricultural yields almost tripled because of the large-scale use of fertilizers and the adoption of high-yielding varieties. These high-yielding varieties were short-statured and had vertically oriented leaves following Donald's ideotype (Donald, 1968). Here, we show how allometric theory can be used to quantify the importance of each driver of increased yield during the Green Revolution.

The total crop yield per unit area is the product of plant density and yield per plant (Deng *et al.*, 2012b):

$$Y = N_{\max} M_{\text{yield}} \tag{Eqn 1}$$

where Y represents the total crop yield produced per unit area that depends on plant density N_{\max} and yield per plant M_{yield} . Metabolic scaling theory (MST) can be used to derive the predicted size–density relationship from the equation of total resource use, which is the product of the number of individuals and resource use per individual (Enquist *et al.*, 1998; Brown *et al.*, 2004):

$$R = N_{\max} Q \tag{Eqn 2}$$

where R is the total resource-use or supply that depends on density N_{\max} and resource-use per plant Q . As the resource-use per individual is predicted to be proportional to growth, $Q \propto M^{3/4}$, this gives (Fig. 5a):

$$R = N_{\max} b_0 M^{3/4} \tag{Eqn 3}$$

$$N_{\max} = \frac{R}{b_0} M^{-3/4} \tag{Eqn 4}$$

where maximal plant density N_{\max} depends on plant size M through a scaling exponent equal to $-3/4$, the resource required for positive growth per unit biomass b_0 , and resource input R . Higher R or lower b_0 results in a higher number of individuals N_{\max} that can be grown per unit area. The yield per plant depends on biomass allocation to the harvestable part and can generally be modelled by an allometric relationship (Pearsall, 1927; Enquist & Niklas, 2002; Niklas & Enquist, 2003; Weiner *et al.*, 2009):

$$M_{\text{yield}} = \alpha M^{\beta} \tag{Eqn 5}$$

where M_{yield} represents the yield per plant that depends on plant size M through a scaling exponent β and a normalization constant α . MST predicts scaling exponents for many vegetative tissues for example $1/4$, $3/4$, for shoot and leaf respectively (Enquist & Niklas, 2002), whereas the scaling exponent for reproductive allocation has no theoretical prediction, varying strongly between species (Weiner, 2004; Weiner *et al.*, 2009).

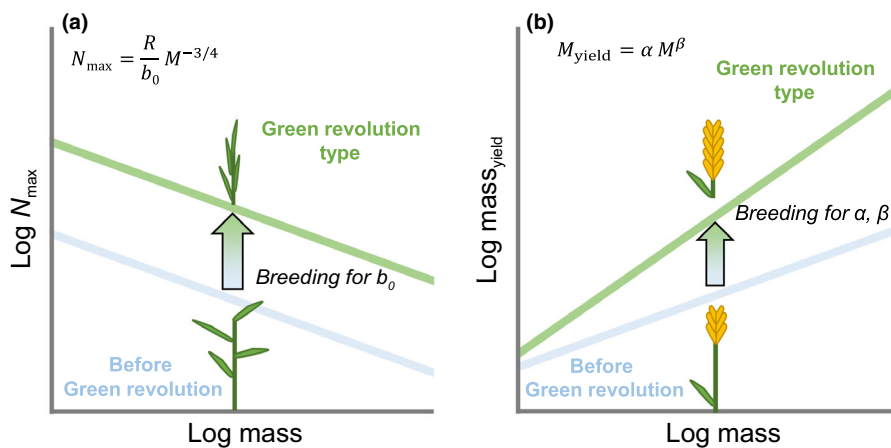


Fig. 5 An allometry perspective on the impact of plant breeding during the Green Revolution. (a) The relationship between plant density (N_{\max}) and plant size (Mass, M) is modelled by an allometric relationship with $-3/4$ scaling exponent β (Deng *et al.*, 2012a,b). Reducing plant resource needs for growth reduces the resource required for positive growth per unit biomass (b_0), thereby increasing maximal planting density for a given plant size. For example, selection for plants with more erect leaves and shorter stems are less competitive and may have allowed increasing plant density and yield during the Green Revolution. Increasing the resource inputs (R) can also increase the number of plants for a given plant size. (b) Plant breeding may also have increased the allocation of biomass to the harvested plant parts by changing the parameters of the allometric relationship (normalization constant α , scaling exponent β) for allocation to the harvested parts (M_{yield}).

This crop model can be used to test how introducing high-yielding varieties and high resource inputs increased yields during the Green Revolution. For example, the introduction of high amounts of artificial fertilizer increased R thereby permitting a higher plant density per unit area (Eqn 4). Breeding for low-competitive genotypes may also have increased plant density by reducing b_0 (Fig. 5a). This may be the case for maize in which yield improvement has been fostered by selecting for density-resistant cultivars with higher light-use efficiency while maintaining the harvest index (Fig. 5a; Duvick, 2005; Lee & Tollenaar, 2007; Perez *et al.*, 2019). The introduction of semi-dwarfs improved biomass allocation to the harvested parts in wheat (Waddington *et al.*, 1986; Evans, 1993; Hay, 1995). This may result from a change in M in combination with a nonlinear relationship with size (Weiner, 2004; Weiner *et al.*, 2009) or by modification of the values of the allometric relationship for biomass allocation (Fig. 5b). A comparison of M , b_0 , α , R , and β across historical series of plant varieties would inform on the relative importance of management vs plant breeding during the Green Revolution. This approach can be extended to evaluate the drivers of yield in other agricultural systems.

a higher plant density per unit area, are susceptible to the invasion of competitive genotypes, known as the tragedy of the commons (Hardin, 1968). Yet, mixing varieties or species in the field may optimize resource uptake and has therefore been proposed to increase yield (Lin, 2011; Litrico & Violle, 2015; Chen *et al.*, 2021). For instance, combining genotypes with different rooting depths may reduce competition for water and nutrients. However, it remains difficult to predict which combination of varieties or species can optimize yield by reducing competition and avoiding the tragedy of the commons. Interestingly, intercropping increased the scaling exponent of reproductive allocation compared with the species in monoculture, resulting in higher allocation rates for larger-sized plants (Gaudio *et al.*, 2021). This suggests that we can improve the reproductive output of one species at a given size when intercropped. As a result, we advocate that allometry can be used to identify the plant sizes for which intercropping is negative, neutral, and positive for reproductive allocation for a species. Importantly, larger plant sizes of the focal species were associated with smaller plant sizes of the associated species (Gaudio *et al.*, 2021). This suggests strong hierarchical competition and may reduce total yield as growing individuals of similar size yields generally higher reproductive mass than growing individuals of very different sizes (Simonsen *et al.*, 2014; Anten & Chen, 2021). Interestingly, the nonlinearity of allometric relationships for reproductive allocation and the associated phenomenon called Jensen's inequality (a recurrent principle as illustrated in Box 2) were used to explain the higher yield in similar-sized individuals (Simonsen *et al.*, 2014; Anten & Chen, 2021). Indeed, increased uniformity between plants of the same genotype has been proposed as a breeding target to increase yield in adverse environments (Borrás & Vitantonio-Mazzini, 2018). These results indicate that large size differences between species or genotypes (i.e. strong hierarchical competition) may increase individual yield of one species but reduce population yield. Thus, using allometry gives insights into the assembly rules of more resource-use-efficient crop cultures.

Conclusion

Assuming that plant size is a major driver of performance at the plant and population level, we advocate here that an allometry perspective on crops is an encouraging avenue for plant breeding and crop modeling that awaits further validation and application.

First, continuing documentation of trait–size relationships, specifically for reproductive traits, at different taxonomic scales will show how allometry shaped crop domestication, and can help identify and predict future evolutionary trajectories (Messina *et al.*, 2011; Milla *et al.*, 2015; Stetter, 2020). Second, studying scaling relationships at the intraspecific level will inform us about the environmental and genetic influences on scaling variation, and will further our capacity to link this variation to performance in the agricultural environment. Finally, a better understanding of crop allometry will allow us to predict yield-related features, such as additive genetic values, heterosis, optimal plant density, and fertilization requirements, thereby helping farmers and breeders in decision-making. Most importantly, we need to perform meta-analyses on a large number of crop species to understand how allometric relationships limit crop evolution. We expect that recent advances in genotyping and phenotyping capacities will allow us to describe scaling relationships and their genetic determinants at different organizational levels. Next, scaling relationships may allow developing complete but simple genotype–phenotype models to predict efficiently plant performance across multiple environments. Moreover, as we still understand limitedly the effects of selection on allometry (Pélabon *et al.*, 2014; Houle *et al.*, 2019), especially in plants, the evaluation of allometries within human-selected crop species is a priority to improve theory and understand the boundaries of phenotypic evolution, a critical question in evolutionary biology (Maynard Smith *et al.*, 1985; Arnold, 1992; Pigliucci, 2007).

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Competing interests

None declared.

Author contributions

AJW wrote the paper with the help of FV, DV and CV. DP, BJE, RM and AG-F provided feedback.

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References

- Aarssen LW, Jordan C. 2001. Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. *Écoscience* 8: 471–477.
- Abbo S, Pinhasi van-Oss R, Gopher A, Saranga Y, Ofner I, Peleg Z. 2014. Plant domestication versus crop evolution: a conceptual framework for cereals and grain legumes. *Trends in Plant Science* 19: 351–360.
- Anfodillo T, Petit G, Sterck F, Lechthaler S, Olson ME. 2016. Allometric trajectories and “stress”: a quantitative approach. *Frontiers in Plant Science* 7: 1681.
- Anten NPR, Chen BJW. 2021. Detect thy family: mechanisms, ecology and agricultural aspects of kin recognition in plants. *Plant, Cell & Environment* 44: 1059–1071.
- Anten NPR, Vermeulen PJ. 2016. Tragedies and crops: understanding natural selection to improve cropping systems. *Trends in Ecology & Evolution* 31: 429–439.
- Arnold SJ. 1992. Constraints on phenotypic evolution. *The American Naturalist* 140: S85–S107.
- Banse K. 1976. Rates of growth, respiration and photosynthesis of unicellular algae as related to cell size – a review. *Journal of Phycology* 12: 135–140.
- Bennett MD. 1987. Variation in genomic form in plants and its ecological implications. *New Phytologist* 106: 177–200.
- Berrocal-Ibarra S, Ortiz-Cereceres J, Peña-Valdivia CB. 2002. Yield components, harvest index and leaf area efficiency of a sample of a wild population and a domesticated variant of the common bean *Phaseolus vulgaris*. *South African Journal of Botany* 68: 205–211.
- Bestová H, Segrestin J, von Schwartzberg K, Škaloud P, Lenormand T, Violle C. 2021. Biological scaling in green algae: the role of cell size and geometry. *Scientific Reports* 11: 14425.
- Bolstad GH, Cassara JA, Márquez E, Hansen TF, van der Linde K, Houle D, Pélabon C. 2015. Complex constraints on allometry revealed by artificial selection on the wing of *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences, USA* 112: 13284–13289.
- Borrás L, Vitantonio-Mazzini LN. 2018. Maize reproductive development and kernel set under limited plant growth environments. *Journal of Experimental Botany* 69: 3235–3243.
- Brisson N, Gary C, Justes E, Roche R, Mary B, Ripoche D, Zimmer D, Sierra J, Bertuzzi P, Burger P *et al.* 2003. An overview of the crop model stics. *European Journal of Agronomy* 18: 309–332.
- Brody S. 1964. *Bioenergetics and growth: with special reference to the efficiency complex in domestic animals*. New York, NY, USA: Hafner.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.
- Calder WA. 1996. *Size, function, and life history*. North Chelmsford, MA, USA: Courier.
- Careau V, Glazier DS. 2022. A quantitative genetics perspective on the body-mass scaling of metabolic rate. *Journal of Experimental Biology* 225: jeb243393.
- Chen J, Engbersen N, Stefan L, Schmid B, Sun H, Schöb C. 2021. Diversity increases yield but reduces harvest index in crop mixtures. *Nature Plants* 7: 893–898.
- Chen ZJ. 2010. Molecular mechanisms of polyploidy and hybrid vigor. *Trends in Plant Science* 15: 57–71.
- Chenu K, Porter JR, Martre P, Basso B, Chapman SC, Ewert F, Bindl M, Asseng S. 2017. Contribution of crop models to adaptation in wheat. *Trends in Plant Science* 22: 472–490.
- Cheverud JM. 1982. Relationships among ontogenetic, static, and evolutionary allometry. *American Journal of Physical Anthropology* 59: 139–149.
- Chmura DJ, Guzicka M, Rozkowski R, Chalupka W. 2017. Allometry varies among related families of Norway spruce. *Annals of Forest Science* 74: 36.
- Coleman JS, McConnaughay KDM, Ackerly DD. 1994. Interpreting phenotypic variation in plants. *Trends in Ecology & Evolution* 9: 187–191.
- Colombié S, Prigent S, Cassan C, Hilbert-Masson G, Renaud C, Dell’Aversana E, Carillo P, Moing A, Beaumont C, Beauvoit B *et al.* 2023. Comparative constraint-based modelling of fruit development across species highlights nitrogen metabolism in the growth-defence trade-off. *The Plant Journal* 116: 786–803.
- Cong B, Barrero LS, Tanksley SD. 2008. Regulatory change in YABBY-like transcription factor led to evolution of extreme fruit size during tomato domestication. *Nature Genetics* 40: 800–804.
- Conner JK. 2003. Artificial selection: a powerful tool for ecologists. *Ecology* 84: 1650–1660.
- Coomes DA, Holdaway RJ, Kobe RK, Lines ER, Allen RB. 2012. A general integrative framework for modelling woody biomass production and carbon sequestration rates in forests. *Journal of Ecology* 100: 42–64.
- Cornelissen JHC. 1999. A triangular relationship between leaf size and seed size among woody species: allometry, ontogeny, ecology and taxonomy. *Oecologia* 118: 248–255.
- Crow JF. 1998. 90 years ago: the beginning of hybrid maize. *Genetics* 148: 923–928.
- Deng J, Ran J, Wang Z, Fan Z, Wang G, Ji M, Liu J, Wang Y, Liu J, Brown JH. 2012a. Models and tests of optimal density and maximal yield for crop plants. *Proceedings of the National Academy of Sciences, USA* 109: 15823–15828.
- Deng J, Zuo W, Wang Z, Fan Z, Ji M, Wang G, Ran J, Zhao C, Liu J, Niklas KJ *et al.* 2012b. Insights into plant size-density relationships from models and agricultural crops. *Proceedings of the National Academy of Sciences, USA* 109: 8600–8605.
- Deng J-M, Li T, Wang G-X, Liu J, Yu Z-L, Zhao C-M, Ji M-F, Zhang Q, Liu J. 2008. Trade-offs between the metabolic rate and population density of plants. *PLoS ONE* 3: e1799.
- Diaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I *et al.* 2016. The global spectrum of plant form and function. *Nature* 529: 167–171.
- Diepenbrock CH, Tang T, Jines M, Technow F, Lira S, Podlich D, Cooper M, Messina C. 2022. Can we harness digital technologies and physiology to hasten genetic gain in US maize breeding? *Plant Physiology* 188: 1141–1157.
- Diez CM, Gaut BS, Meca E, Scheinvar E, Montes-Hernandez S, Eguarte LE, Tenaillon MI. 2013. Genome size variation in wild and cultivated maize along altitudinal gradients. *New Phytologist* 199: 264–276.
- Dodds PS, Rothman DH, Weitz JS. 2001. Re-examination of the “3/4-law” of metabolism. *Journal of Theoretical Biology* 209: 9–27.
- Donald CM. 1968. The breeding of crop ideotypes. *Euphytica* 17: 385–403.
- Du Y-L, Xi Y, Cui T, Anten NPR, Weiner J, Li X, Turner NC, Zhao Y-M, Li F-M. 2020. Yield components, reproductive allometry and the tradeoff between grain yield and yield stability in dryland spring wheat. *Field Crops Research* 257: 107930.
- Dunstone RL, Evans LT. 1974. Role of changes in cell size in the evolution of wheat. *Functional Plant Biology* 1: 157–165.
- Duursma RA, Mäkelä A, Reid DEB, Jokela EJ, Porté AJ, Roberts SD. 2010. Self-shading affects allometric scaling in trees: self-shading and allometric scaling. *Functional Ecology* 24: 723–730.
- Duvick DN. 2005. The contribution of breeding to yield advances in maize (*Zea mays* L.). In: Sparks DN, ed. *Advances in agronomy*. San Diego, CA, USA: Academic Press, 83–145.
- Egset CK, Hansen TF, Rouzic AL, Bolstad GH, Rosenqvist G, Pélabon C. 2012. Artificial selection on allometry: change in elevation but not slope. *Journal of Evolutionary Biology* 25: 938–948.
- Elgin M. 2006. There may be strict empirical laws in biology, after all. *Biology and Philosophy* 21: 119–134.
- Enquist BJ. 2002. Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiology* 22: 1045–1064.

- Enquist BJ, Allen AP, Brown JH, Gillooly JF, Kerkhoff AJ, Niklas KJ, Price CA, West GB. 2007. Does the exception prove the rule? *Nature* 445: E9–E10.
- Enquist BJ, Bentley LP. 2012. Land plants: new theoretical directions and empirical prospects. In: Sibly RM, Brown JH, Kodric-Brown A, eds. *Metabolic ecology*. Chichester, UK: John Wiley & Sons, 164–187.
- Enquist BJ, Brown JH, West GB. 1998. Allometric scaling of plant energetics and population density. *Nature* 395: 163–165.
- Enquist BJ, Niklas KJ. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295: 1517–1520.
- Enquist BJ, West GB, Brown JH. 2000. Quarter-power allometric scaling in vascular plants: functional basis and ecological consequences. In: Brown JH, West GB, eds. *Scaling in biology*. Oxford, UK: Oxford University Press, 167–198.
- Enquist BJ, West GB, Charnov EL, Brown JH. 1999. Allometric scaling of production and life-history variation in vascular plants. *Nature* 401: 907–911.
- Evans L, Dunstone R. 1970. Some physiological aspects of evolution in wheat. *Australian Journal of Biological Sciences* 23: 725.
- Evans LT. 1993. *Crop evolution, adaptation and yield*. Cambridge, UK: Cambridge University Press.
- Evvin A, Dobney K, Schafberg R, Owen J, Vidarsdottir US, Larson G, Cucchi T. 2015. Phenotype and animal domestication: a study of dental variation between domestic, wild, captive, hybrid and insular *Sus scrofa*. *BMC Evolutionary Biology* 15: 6.
- Eziz A, Yan Z, Tian D, Han W, Tang Z, Fang J. 2017. Drought effect on plant biomass allocation: a meta-analysis. *Ecology and Evolution* 7: 11002–11010.
- Fang Z, Morrell PL. 2016. Domestication: polyploidy boosts domestication. *Nature Plants* 2: 1–2.
- Fiévet JB, Nidelet T, Dillmann C, de Vienne D. 2018. Heterosis is a systemic property emerging from non-linear genotype-phenotype relationships: evidence from *in vitro* genetics and computer simulations. *Frontiers in Genetics* 9: 159.
- Flood PJ, Kruijer W, Schnabel SK, van der Schoor R, Jalink H, Snel JFH, Harbinson J, Aarts MGM. 2016. Phenomics for photosynthesis, growth and reflectance in *Arabidopsis thaliana* reveals circadian and long-term fluctuations in heritability. *Plant Methods* 12: 14.
- Fournier M-P, Paré MC, Buttó V, Delagrangé S, Lafond J, Deslauriers A. 2020. How plant allometry influences bud phenology and fruit yield in two *Vaccinium* species. *Annals of Botany* 126: 825–835.
- Frankino WA, Zwaan BJ, Stern DL, Brakefield PM. 2005. Natural selection and developmental constraints in the evolution of allometries. *Science* 307: 718–720.
- Fuller DQ. 2012. New archaeobotanical information on plant domestication from macro-remains: tracking the evolution of domestication syndrome traits. In: Damania AB, Qalset CO, McGuire PE, Gepts P, Bettinger RL, Brush SB, Famula TR, eds. *Biodiversity in agriculture: domestication, evolution, and sustainability*. Cambridge, UK: Cambridge University Press, 110–135.
- Gaudio N, Violle C, Gendreau X, Fort F, Mahmoud R, Pelzer E, Médiène S, Hauggaard-Nielsen H, Bedoussac L, Bonnet C *et al.* 2021. Interspecific interactions regulate plant reproductive allometry in cereal–legume intercropping systems. *Journal of Applied Ecology* 58: 2579–2589.
- Glazier DS. 2005. Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews* 80: 611–662.
- Glazier DS. 2014. Metabolic scaling in complex living systems. *Systems* 2: 451–540.
- Glazier DS. 2022. Variable metabolic scaling breaks the law: from 'Newtonian' to 'Darwinian' approaches. *Proceedings of the Royal Society B: Biological Sciences* 289: 20221605.
- Golan G, Weiner J, Zhao Y, Schnurbusch T. 2024. Agroecological genetics of biomass allocation in wheat uncovers genotype interactions with canopy shade and plant size. *New Phytologist* 242: 107–120.
- Gómez-Fernández A, Milla R. 2022. How seeds and growth dynamics influence plant size and yield: integrating trait relationships into ontogeny. *Journal of Ecology* 110: 2684–2700.
- Gómez-Fernández A, Osborne CP, Rees M, Palomino J, Ingala C, Gómez G, Milla R. 2022. Disparities among crop species in the evolution of growth rates: the role of distinct origins and domestication histories. *New Phytologist* 233: 995–1010.
- González-Paleo L, Ravetta DA. 2012. Allocation patterns and phenology in wild and selected accessions of annual and perennial *Physaria* (Lesquerella, Brassicaceae). *Euphytica* 186: 289–302.
- Gould SJ. 1966. Allometry and size in ontogeny and phylogeny. *Biological Reviews of the Cambridge Philosophical Society* 41: 587–640.
- Granier C, Aguirrezabal L, Chenu K, Cookson SJ, Dauzat M, Hamard P, Thioux J-J, Rolland G, Bouchier-Combaud S, Lebaudy A *et al.* 2006. PHENOPSIS, an automated platform for reproducible phenotyping of plant responses to soil water deficit in *Arabidopsis thaliana* permitted the identification of an accession with low sensitivity to soil water deficit. *New Phytologist* 169: 623–635.
- Gregory TR. 2002. A bird's-eye view of the C-value enigma: genome size, cell size, and metabolic rate in the class aves. *Evolution* 56: 121–130.
- Guo M, Rupe MA, Dieter JA, Zou J, Spielbauer D, Duncan KE, Howard RJ, Hou Z, Simmons CR. 2010. Cell Number Regulator1 affects plant and organ size in maize: implications for crop yield enhancement and heterosis. *Plant Cell* 22: 1057–1073.
- Hammer G, Cooper M, Tardieu F, Welch S, Walsh B, van Eeuwijk F, Chapman S, Podlich D. 2006. Models for navigating biological complexity in breeding improved crop plants. *Trends in Plant Science* 11: 587–593.
- Hammer G, Messina C, Wu A, Cooper M. 2019. Biological reality and parsimony in crop models – why we need both in crop improvement! *In Silico Plants* 1: diz010.
- Hammer GL, van Oosterom E, McLean G, Chapman SC, Broad I, Harland P, Muchow RC. 2010. Adapting APSIM to model the physiology and genetics of complex adaptive traits in field crops. *Journal of Experimental Botany* 61: 2185–2202.
- Hammer K. 1984. Das domestikationssyndrom. *Die Kulturpflanze* 32: 11–34.
- Hardin G. 1968. The tragedy of the commons. *Science* 162: 1243–1248.
- Hay RKM. 1995. Harvest index: a review of its use in plant breeding and crop physiology. *Annals of Applied Biology* 126: 197–216.
- He T, Angessa TT, Li C. 2023. Pleiotropy structures plant height and seed weight scaling in barley despite long history of domestication and breeding selection. *Plant Phenomics* 5: 0015.
- Heck L, Sanchez-Villagra MR, Stange M. 2019. Why the long face? Comparative shape analysis of miniature, pony, and other horse skulls reveals changes in ontogenetic growth. *PeerJ* 7: e7678.
- Hedden P. 2003. The genes of the Green Revolution. *Trends in Genetics* 19: 5–9.
- Houle D, Jones LT, Fortune R, Sztepanacz JL. 2019. Why does allometry evolve so slowly? *Integrative and Comparative Biology* 59: 1429–1440.
- Huang Z, Tong C, Bo W, Pang X, Wang Z, Xu J, Gai J, Wu R. 2014. An allometric model for mapping seed development in plants. *Briefings in Bioinformatics* 15: 562–570.
- Huxley JS. 1924. Constant differential growth-ratios and their significance. *Nature* 114: 895–896.
- Huxley JS. 1932. *Problems of relative growth*. New York, NY, USA: L. MacVeagh, The Dial Press.
- Jennings PR, de Jesus J. 1968. Studies on competition in rice I. Competition in mixtures of varieties. *Evolution* 22: 119–124.
- Jiang L, Ye M, Zhu S, Zhai Y, Xu M, Huang M, Wu R. 2016. Computational identification of genes modulating stem height–diameter allometry. *Plant Biotechnology Journal* 14: 2254–2264.
- John GP, Scoffoni C, Sack L. 2013. Allometry of cells and tissues within leaves. *American Journal of Botany* 100: 1936–1948.
- Jones JW, Hoogenboom G, Porter CH, Boote KJ, Batchelor WD, Hunt LA, Wilkens PW, Singh U, Gijsman AJ, Ritchie JT. 2003. The DSSAT cropping system model. *European Journal of Agronomy* 18: 235–265.
- Keating BA, Carberry PS, Hammer GL, Probert ME, Robertson MJ, Holzworth D, Huth NI, Hargreaves JNG, Meinke H, Hochman Z *et al.* 2003. An overview of APSIM, a model designed for farming systems simulation. *European Journal of Agronomy* 18: 267–288.
- Kempes CP, Koehl MAR, West GB. 2019. The scales that limit: the physical boundaries of evolution. *Frontiers in Ecology and Evolution* 7: 242.
- Khush GS. 1999. Green revolution: preparing for the 21st century. *Genome* 42: 646–655.
- Kleiber M. 1932. Body size and metabolism. *Hilgardia* 6: 315–353.
- Kleiber M. 1947. Body size and metabolic rate. *Physiological Reviews* 27: 511–541.
- Kluyver TA, Jones G, Pujol B, Bennett C, Mockford EJ, Charles M, Rees M, Osborne CP. 2017. Unconscious selection drove seed enlargement in vegetable crops. *Evolution Letters* 1: 64–72.
- Knight CA, Beaulieu JM. 2008. Genome size scaling through phenotype space. *Annals of Botany* 101: 759–766.
- Kolokotronis T, Savage V, Deeds EJ, Fontana W. 2010. Curvature in metabolic scaling. *Nature* 464: 753–756.

- Kozłowski J, Konarzewski M, Czarnoleski M. 2020. Coevolution of body size and metabolic rate in vertebrates: a life-history perspective. *Biological Reviews* 95: 1393–1417.
- Kozłowski J, Konarzewski M, Gawelczyk AT. 2003. Cell size as a link between noncoding DNA and metabolic rate scaling. *Proceedings of the National Academy of Sciences, USA* 100: 14080–14085.
- LaBarbera M. 1989. Analyzing body size as a factor in ecology and evolution. *Annual Review of Ecology and Systematics* 20: 97–117.
- Lee EA, Tollenaar M. 2007. Physiological basis of successful breeding strategies for maize grain yield. *Crop Science* 47: S-202–S-215.
- Lemaire G, Sinclair T, Sadras V, Bélanger G. 2019. Allometric approach to crop nutrition and implications for crop diagnosis and phenotyping. A review. *Agronomy for Sustainable Development* 39: 27.
- Li H, Huang Z, Gai J, Wu S, Zeng Y, Li Q, Wu R. 2007. A conceptual framework for mapping quantitative trait loci regulating ontogenetic allometry. *PLoS ONE*: e1245.
- Li L, Bonser SP, Lan Z, Xu L, Chen J, Song Z. 2017. Water depth affects reproductive allocation and reproductive allometry in the submerged macrophyte *Vallisneria spiralis*. *Scientific Reports* 7: 16842.
- Lim SD, Yim WC, Liu D, Hu R, Yang X, Cushman JC. 2018. A *Vitis vinifera* basic helix–loop–helix transcription factor enhances plant cell size, vegetative biomass and reproductive yield. *Plant Biotechnology Journal* 16: 1595–1615.
- Lin BB. 2011. Resilience in agriculture through crop diversification: adaptive management for environmental change. *Bioscience* 61: 183–193.
- Litrico I, Violle C. 2015. Diversity in plant breeding: a new conceptual framework. *Trends in Plant Science* 20: 604–613.
- Long F, Qing Chen Y, Cheverud JM, Wu R. 2006. Genetic mapping of allometric scaling laws. *Genetical Research* 87: 207–216.
- Ma C-X, Casella G, Wu R. 2002. Functional mapping of quantitative trait loci underlying the character process: a theoretical framework. *Genetics* 161: 1751–1762.
- Marba N, Duarte CM, Agusti S. 2007. Allometric scaling of plant life history. *Proceedings of the National Academy of Sciences, USA* 104: 15777–15780.
- Marcelis LFM, Heuvelink E, Goudriaan J. 1998. Modelling biomass production and yield of horticultural crops: a review. *Scientia Horticulturae* 74: 83–111.
- Martre P, Porter JR, Jamieson PD, Tribou E. 2003. Modeling grain nitrogen accumulation and protein composition to understand the sink/source regulations of nitrogen remobilization for wheat. *Plant Physiology* 133: 1959–1967.
- Maynard Smith J, Burian R, Kauffman S, Alberch P, Campbell J, Goodwin B, Lande R, Raup D, Wolpert L. 1985. Developmental constraints and evolution: a perspective from the mountain lake conference on development and evolution. *The Quarterly Review of Biology* 60: 265–287.
- Mccarthy MC, Enquist BJ. 2007. Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology* 21: 713–720.
- McConaughay KDM, Coleman JS. 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* 80: 2581–2593.
- McMahon TA, Bonner JT. 1983. *On size and life*. New York, NY, USA: Scientific American Library.
- Messina C, Hammer G, Dong Z, Podlich D, Cooper M. 2009. Chapter 10 – Modelling crop improvement in a G×E×M framework via gene–trait–phenotype relationships. In: Sadras V, Calderini D, eds. *Crop physiology*. San Diego, CA, USA: Academic Press, 235–581.
- Messina CD, Gho C, Hammer GL, Tang T, Cooper M. 2023. Two decades of harnessing standing genetic variation for physiological traits to improve drought tolerance in maize. *Journal of Experimental Botany* 74: 4847–4861.
- Messina CD, Podlich D, Dong Z, Samples M, Cooper M. 2011. Yield–trait performance landscapes: from theory to application in breeding maize for drought tolerance. *Journal of Experimental Botany* 62: 855–868.
- Messina CD, Van Eeuwijk F, Tang T, Truong SK, McCormick RF, Technow F, Powell O, Mayor L, Gutterson N, Jones JW *et al.* 2022. Crop improvement for circular bioeconomy systems. *Journal of the ASABE* 65: 491–504.
- Meyer RS, DuVal AE, Jensen HR. 2012. Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytologist* 196: 29–48.
- Milla R, Matesanz S. 2017. Growing larger with domestication: a matter of physiology, morphology or allocation? *Plant Biology* 19: 475–483.
- Milla R, Morente-López J, Alonso-Rodrigo JM, Martín-Robles N, Stuart CF. 2014. Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proceedings of the Royal Society B: Biological Sciences* 281: 20141429.
- Milla R, Osborne CP, Turcotte MM, Violle C. 2015. Plant domestication through an ecological lens. *Trends in Ecology & Evolution* 30: 463–469.
- Milla R, Westgeest AJ, Maestre-Villanueva J, Núñez-Castillo S, Gómez-Fernández A, Vasseur F, Violle C, Balarynová J, Smykal P. 2024. Evolutionary pathways to lower biomass allocation to the seed coat in crops: insights from allometric scaling. *New Phytologist* 243: 466–476.
- Montazeaud G, Rousset F, Fort F, Violle C, Fréville H, Gandon S. 2020. Farming plant cooperation in crops. *Proceedings of the Royal Society B: Biological Sciences* 287: 20191290.
- Monteith JL. 1977. Climate and the efficiency of crop production in Britain [and discussion]. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 281: 277–294.
- Mori S, Yamaji K, Ishida A, Prokushkin SG, Masyagina OV, Hagihara A, Hoque ATMR, Suwa R, Osawa A, Nishizono T *et al.* 2010. Mixed-power scaling of whole-plant respiration from seedlings to giant trees. *Proceedings of the National Academy of Sciences, USA* 107: 1447–1451.
- Mowforth MA, Grime JP. 1989. Intra-population variation in nuclear DNA amount, cell size and growth rate in *Poa annua* L. *Functional Ecology* 3: 289–295.
- Mueller RL. 2015. Genome biology and the evolution of cell-size diversity. *Cold Spring Harbor Perspectives in Biology* 7: a019125.
- Muir CD, Thomas-Huebner M. 2015. Constraint around quarter-power allometric scaling in wild tomatoes (*Solanum* sect. *Lycopersicon*; Solanaceae). *The American Naturalist* 186: 421–433.
- Nicolas P, Lecourieux D, Gomès E, Delrot S, Lecourieux F. 2013. The grape berry-specific basic helix–loop–helix transcription factor VvCEB1 affects cell size. *Journal of Experimental Botany* 64: 991–1003.
- Niklas KJ. 1994. *Plant allometry: the scaling of form and process*. Chicago, IL, USA: University of Chicago Press.
- Niklas KJ. 1995. Size-dependent allometry of tree height, diameter and trunk-taper. *Annals of Botany* 75: 217–227.
- Niklas KJ. 2006. Plant allometry, leaf nitrogen and phosphorus stoichiometry, and interspecific trends in annual growth rates. *Annals of Botany* 97: 155–163.
- Niklas KJ, Enquist BJ. 2001. Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proceedings of the National Academy of Sciences, USA* 98: 2922–2927.
- Niklas KJ, Enquist BJ. 2002. Canonical rules for plant organ biomass partitioning and annual allocation. *American Journal of Botany* 89: 812–819.
- Niklas KJ, Enquist BJ. 2003. An allometric model for seed plant reproduction. *Evolutionary Ecology Research* 5: 78–88.
- Niklas KJ, Marler TE. 2007. *Carica papaya* (Caricaceae): a case study into the effects of domestication on plant vegetative growth and reproduction. *American Journal of Botany* 94: 999–1002.
- Normand F, Lauri P-É. 2012. Assessing allometric models to predict vegetative growth of mango (*Mangifera indica*; Anacardiaceae) at the current-year branch scale. *American Journal of Botany* 99: 425–437.
- Núñez-León D, Cordero GA, Schindweng X, Jensen P, Stoeckli E, Sánchez-Villagra MR, Werneburg I. 2021. Shifts in growth, but not differentiation, foreshadow the formation of exaggerated forms under chicken domestication. *Proceedings of the Royal Society B: Biological Sciences* 288: 20210392.
- Olson ME. 2012. The developmental renaissance in adaptationism. *Trends in Ecology & Evolution* 27: 278–287.
- Onogi A. 2022. Integration of crop growth models and genomic prediction. In: Ahmadi N, Bartholomé J, eds. *Methods in molecular biology. Genomic prediction of complex traits: methods and protocols*. New York, NY, USA: Springer US, 359–396.
- Pearsall WH. 1927. Growth studies. VI. On the relative sizes of growing plant organs. *Annals of Botany* 41: 549–556.
- Peaucelle M, Bacour C, Ciais P, Vuichard N, Kuppel S, Peñuelas J, Beileli Marchesini L, Blanken PD, Buchmann N, Chen J *et al.* 2019. Covariations between plant functional traits emerge from constraining parameterization of a terrestrial biosphere model. *Global Ecology and Biogeography* 28: 1351–1365.
- Pedrosa HC, Clement CR, Schietti J. 2018. The domestication of the Amazon tree grape (*Pourouma cecropifolia*) under an ecological lens. *Frontiers in Plant Science* 9: 203.

- Pélabon C, Firmat C, Bolstad GH, Voje KL, Houle D, Cassara J, Rouzic AL, Hansen TF. 2014. Evolution of morphological allometry. *Annals of the New York Academy of Sciences* 1320: 58–75.
- Perez RPA, Fournier C, Cabrera-Bosquet L, Artzet S, Pradal C, Brichet N, Chen T, Chapuis R, Welcker C, Tardieu F. 2019. Changes in the vertical distribution of leaf area enhanced light interception efficiency in maize over generations of selection. *Plant, Cell & Environment* 42: 2105–2119.
- Peters RH. 1983. *The ecological implications of body size*. Cambridge, UK: Cambridge University Press.
- Pigliucci M. 2007. Finding the way in phenotypic space: the origin and maintenance of constraints on organismal form. *Annals of Botany* 100: 433–438.
- Plessis A, Ravel C, Bordes J, Balfourier F, Martre P. 2013. Association study of wheat grain protein composition reveals that gliadin and glutenin composition are trans-regulated by different chromosome regions. *Journal of Experimental Botany* 64: 3627–3644.
- Poorter H, Jagodzinski AM, Ruiz-Peinado R, Kuyah S, Luo Y, Oleksyn J, Usoltsev VA, Buckley TN, Reich PB, Sack L. 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist* 208: 736–749.
- Poorter H, Sack L. 2012. Pitfalls and possibilities in the analysis of biomass allocation patterns in plants. *Frontiers in Plant Science* 3: 259.
- Price CA, Enquist BJ, Savage VM. 2007. A general model for allometric covariation in botanical form and function. *Proceedings of the National Academy of Sciences, USA* 104: 13204–13209.
- Price CA, Gilooly JF, Allen AP, Weitz JS, Niklas KJ. 2010. The metabolic theory of ecology: prospects and challenges for plant biology. *New Phytologist* 188: 696–710.
- Qin X, Weiner J, Qi L, Xiong Y, Li F. 2013. Allometric analysis of the effects of density on reproductive allocation and Harvest Index in 6 varieties of wheat (*Triticum*). *Field Crops Research* 144: 162–166.
- Qin X, Zhang F, Wang M, Shi C, Liao Y, Wen X, Siddique KHM. 2016. The scaling relationship of below and above-ground biomass of different grain crops during the seedling stage. *International Journal of Agriculture and Biology* 18: 584–588.
- Reich PB. 2001. Body size, geometry, longevity and metabolism: do plant leaves behave like animal bodies? *Trends in Ecology & Evolution* 16: 674–680.
- Reich PB, Tjoelker MG, Machado J-L, Oleksyn J. 2006. Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature* 439: 457–461.
- Reynolds D, Baret F, Welcker C, Bostrom A, Ball J, Cellini F, Lorence A, Chawade A, Khafif M, Noshita K *et al.* 2019. What is cost-efficient phenotyping? Optimizing costs for different scenarios. *Plant Science* 282: 14–22.
- Roddy AB, Thérout-Rancourt G, Abbo T, Benedetti JW, Brodersen CR, Castro M, Castro S, Gilbride AB, Jensen B, Jiang G-F *et al.* 2020. The scaling of genome size and cell size limits maximum rates of photosynthesis with implications for ecological strategies. *International Journal of Plant Sciences* 181: 75–87.
- Rotundo JL, Borrás L, Westgate ME, Orf JH. 2009. Relationship between assimilate supply per seed during seed filling and soybean seed composition. *Field Crops Research* 112: 90–96.
- Roucou A, Violle C, Fort F, Roumet P, Ecartot M, Vile D. 2018. Shifts in plant functional strategies over the course of wheat domestication. *Journal of Applied Ecology* 55: 25–37.
- Royo C, Ammar K, Villegas D, Soriano JM. 2021. Agronomic, physiological and genetic changes associated with evolution, migration and modern breeding in durum wheat. *Frontiers in Plant Science* 12: 674470.
- Rubner M. 1883. Ueber den einfluss der korpergrösse auf stoffund kaftwechsel. *Zeitschrift für Biologie* 19: 535–562.
- Sadras VO, Lemaire G. 2014. Quantifying crop nitrogen status for comparisons of agronomic practices and genotypes. *Field Crops Research* 164: 54–64.
- Salman-Minkov A, Sabath N, Mayrose I. 2016. Whole-genome duplication as a key factor in crop domestication. *Nature Plants* 2: 1–4.
- Samson DA, Werk KS. 1986. Size-dependent effects in the analysis of reproductive effort in plants. *The American Naturalist* 127: 667–680.
- Sánchez-Villagra MR, Segura V, Geiger M, Heck L, Veitschegger K, Flores D. 2017. On the lack of a universal pattern associated with mammalian domestication: differences in skull growth trajectories across phylogeny. *Royal Society Open Science* 4: 170876.
- Savage VM, Bentley LP, Enquist BJ, Sperry JS, Smith DD, Reich PB, von Allmen EI. 2010. Hydraulic trade-offs and space filling enable better predictions of vascular structure and function in plants. *Proceedings of the National Academy of Sciences, USA* 107: 22722–22727.
- Schmidt-Nielsen K. 1984. *Scaling: why is animal size so important?* Cambridge, UK: Cambridge University Press.
- Schwanitz F. 1967. *The evolution of cultivated plants*. Cambridge, UK: Harvard University Press.
- Semchenko M, Zobel K. 2005. The effect of breeding on allometry and phenotypic plasticity in four varieties of oat (*Avena sativa* L.). *Field Crops Research* 93: 151–168.
- Simonsen AK, Chow T, Stinchcombe JR. 2014. Reduced plant competition among kin can be explained by Jensen's inequality. *Ecology and Evolution* 4: 4454–4466.
- Simpson KJ, Wade RN, Rees M, Osborne CP, Hartley SE. 2017. Still armed after domestication? Impacts of domestication and agronomic selection on silicon defences in cereals. *Functional Ecology* 31: 2108–2117.
- Sinervo B, Huey RB. 1990. Allometric engineering: an experimental test of the causes of interpopulational differences in performance. *Science* 248: 1106–1109.
- Soltani A, Maddah V, Sinclair TR. 2013. SSM-wheat: a simulation model for wheat development, growth and yield. *International Journal of Plant Production* 7: 711–740.
- Sousa T, Domingos T, Kooijman SA. 2008. From empirical patterns to theory: a formal metabolic theory of life. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 363: 2453–2464.
- Starostová Z, Kubička L, Konarzewski M, Kozłowski J, Kratochvíl L. 2009. Cell size but not genome size affects scaling of metabolic rate in eyelid geckos. *The American Naturalist* 174: E100–E105.
- Stetter MG. 2020. Limits and constraints to crop domestication. *American Journal of Botany* 107: 1617–1621.
- Tamagno S, Sadras VO, Ortez OA, Ciampitti IA. 2020. Allometric analysis reveals enhanced reproductive allocation in historical set of soybean varieties. *Field Crops Research* 248: 107717.
- Tardieu F, Cabrera-Bosquet L, Pridmore T, Bennett M. 2017. Plant phenomics, from sensors to knowledge. *Current Biology* 27: R770–R783.
- Technow F, Messina CD, Totir LR, Cooper M. 2015. Integrating crop growth models with whole genome prediction through approximate Bayesian computation. *PLoS ONE* 10: e0130855.
- Tenaillon MI, Hufford MB, Gaut BS, Ross-Ibarra J. 2011. Genome size and transposable element content as determined by high-throughput sequencing in maize and *Zea luxurians*. *Genome Biology and Evolution* 3: 219–229.
- Vasseur F, Exposito-Alonso M, Ayala-Garay OJ, Wang G, Enquist BJ, Vile D, Violle C, Weigel D. 2018. Adaptive diversification of growth allometry in the plant *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences, USA* 115: 3416–3421.
- Vasseur F, Fouqueau L, De Vienne D, Nidelet T, Violle C, Weigel D. 2019. Nonlinear phenotypic variation uncovers the emergence of heterosis in *Arabidopsis thaliana*. *PLoS Biology* 17: e3000214.
- Vasseur F, Violle C, Enquist BJ, Granier C, Vile D. 2012. A common genetic basis to the origin of the leaf economics spectrum and metabolic scaling allometry. *Ecology Letters* 15: 1149–1157.
- Vasseur F, Westgeest AJ, Vile D, Violle C. 2022. Solving the grand challenge of phenotypic integration: allometry across scales. *Genetica* 150: 161–169.
- Vavilov NI. 1951. *The origin, variation, immunity and breeding of cultivated plants*. London, UK: Wm. Dawson and Sons.
- Vega CRC, Sadras VO, Andrade FH, Uhart SA. 2000. Reproductive allometry in soybean, maize and sunflower. *Annals of Botany* 85: 461–468.
- Vicente MH, MacLeod K, Zhu F, Rafael DD, Figueira A, Fernie AR, Mohareb F, Kevei Z, Thompson AJ, Zsögön A *et al.* 2023. The ORGAN SIZE (ORG) locus modulates both vegetative and reproductive gigantism in domesticated tomato. *Annals of Botany* 132: 1233–1248.
- Violle C, Garnier E, Lecoecur J, Roumet C, Pouteur C, Blanchard A, Navas M-L. 2009. Competition, traits and resource depletion in plant communities. *Oecologia* 160: 747–755.
- Voje KL, Hansen TF, Egset CK, Bolstad GH, Pélabon C. 2014. Allometric constraints and the evolution of allometry. *Evolution* 68: 866–885.
- Volpato L, Pinto F, González-Pérez L, Thompson IG, Borém A, Reynolds M, Gérard B, Molero G, Rodrigues FA. 2021. High throughput field phenotyping for plant height using UAV-based RGB imagery in wheat breeding lines: feasibility and validation. *Frontiers in Plant Science* 12: 591587.

- Waddington SR, Ransom JK, Osmanzai M, Saunders DA. 1986. Improvement in the yield potential of bread wheat adapted to Northwest Mexico. *Crop Science* 26: 698–703.
- Wang Y, Donovan LA, Temme AA. 2020. Plasticity and the role of mass-scaling in allocation, morphology, and anatomical trait responses to above- and belowground resource limitation in cultivated sunflower (*Helianthus annuus* L.). *Plant Direct* 4: e00274.
- Warton DI, Duursma RA, Falster DS, Taskinen S. 2012. SMATR 3 – an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution* 3: 257–259.
- Weiner J. 2004. Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 207–215.
- Weiner J. 2019. Looking in the wrong direction for higher-yielding crop genotypes. *Trends in Plant Science* 24: 927–933.
- Weiner J, Andersen SB, Wille WK-M, Griepentrog HW, Olsen JM. 2010. Evolutionary agroecology: the potential for cooperative, high density, weed-suppressing cereals. *Evolutionary Applications* 3: 473–479.
- Weiner J, Campbell LG, Pino J, Echarte L. 2009. The allometry of reproduction within plant populations. *Journal of Ecology* 97: 1220–1233.
- Weiner J, Du Y-L, Zhao Y-M, Li F-M. 2021. Allometry and yield stability of cereals. *Frontiers in Plant Science* 12: 681490.
- West GB, Brown JH, Enquist BJ. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276: 122–126.
- West GB, Brown JH, Enquist BJ. 1999a. The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* 284: 1677–1679.
- West GB, Brown JH, Enquist BJ. 1999b. A general model for the structure and allometry of plant vascular systems. *Nature* 400: 664–667.
- West GB, Enquist BJ, Brown JH. 2009. A general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences, USA* 106: 7040–7045.
- White CR. 2010. There is no single p. *Nature* 464: 691–693.
- White CR, Alton LA, Bywater CL, Lombardi EJ, Marshall DJ. 2022. Metabolic scaling is the product of life-history optimization. *Science* 377: 834–839.
- White J. 1981. The allometric interpretation of the self-thinning rule. *Journal of Theoretical Biology* 89: 475–500.
- Wilkins O, Nahal H, Foong J, Provart NJ, Campbell MM. 2009. Expansion and diversification of the *Populus* R2R3-MYB family of transcription factors. *Plant Physiology* 149: 981–993.
- Wright S. 1934. Physiological and evolutionary theories of dominance. *The American Naturalist* 68: 24–53.
- Wuest SE, Pires ND, Luo S, Vasseur F, Messier J, Grossniklaus U, Niklaus PA. 2022. Increasing plant group productivity through latent genetic variation for cooperation. *PLoS Biology* 20: e3001842.
- Zhang H, Cao Y, Wang Z, Ye M, Wu R. 2023. Functional mapping of genes modulating plant shade avoidance using leaf traits. *Plants* 12: 608.
- Zhang M, Zhang S, Ye M, Jiang L, Vallejos CE, Wu R. 2020. The genetic control of leaf allometry in the common bean, *Phaseolus vulgaris*. *BMC Genetics* 21: 29.
- Zheng B, Chenu K, Doherty AW, Chapman S. 2014. *The APSIM-wheat module (7.5 R3008)*. Toowoomba, Australia: APSRU unit, 1–44.
- Zhou X, Yang M, Liu Z, Li P, Xie B, Peng C. 2021. Dynamic allometric scaling of tree biomass and size. *Nature Plants* 7: 42–49.
- Zhu X-G, Long SP, Ort DR. 2010. Improving photosynthetic efficiency for greater yield. *Annual Review of Plant Biology* 61: 235–261.